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**CORTICAL MECHANISMS OF THE ORIENTING REFLEX
AND ITS RELATION TO THE CONDITIONED REFLEX.**

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A distinguishing peculiarity of the changes in the human electroencephalogram, induced by various stimuli is that these responses gradually disappear with continued presentation of both indifferent and conditioned stimuli. This phenomenon, known in electrophysiology by the descriptive term of "habituation" is attracting increasing attention of numerous investigators (Sharpless and Jasper, 1956; Jouvet and Hernandez-Peon, 1957; Gastaut and others, 1957; Ricci, Doane and Jasper, 1957). Despite the great attention they are enjoying these mechanisms are still wanting a fuller explanation.

This paper concentrates on the analysis of the extinction mechanism of the alpha-rhythm blockade in man made by a study of the data obtained through the complex recording of the alpha-rhythm of the occipital and motor areas, the skin-galvanic reaction, the changes in respiration, movements of the eye, and the muscular responses (L.G.Voronin, E.N.Sokolov, 1955, 1958; E.N.Sokolov, 1955, 1958). The induced by sound, tactile, proprioceptive and

light . . . was stimuli. A projection perimeter which enabled to present local stimulation by light to various points of the retina was used to investigate the generalisation during the extinction of the electrical brain reaction. In a number of tests the automatic frequency analysis of the electroencephalograms was employed to define the changes associated with the development of inhibition during the extinction of the alpha-rhythm blockade reaction. To study the changes in the functional state of the cortex during the extinction process "driving response" induced by the flicker light was also used.

I. Blockade or Alpha-rhythm Activation as a Component of the Orienting Reflex.

The recording of the variations in the electrical activity of the occipital and the motor area, of the skin-galvanic reaction, of the eye movements, the respiration movements and of the muscular tonus reveal that a new stimulus simultaneously induces a variety of reactions with a common feature being their participation in the activation of the organism and in the tuning of the receptory apparatus. Together with the alpha-rhythm blockade there takes place the turn of the eyes towards the source of sound, light or the tactile stimulation, there appears a respiratory delay, a skin-galvanic reaction and there might be an increase in the muscular tonus.

A characteristic feature of the above-said somatic and vegetative reaction, is that they regularly become extinct

and are reinstated when a new stimulus is applied or the conditions of the presentation are altered.

The form of the brain electrical response is subject to the initial background. Since the development of sleep inhibition, which is characteristic of a drop in the electrical brain activity and the appearance of the delta and theta waves, the stimulation also induces the movement of the eyes, a skin-galvanic reaction and an alteration in the respiration, but all of them are accompanied by the activation of the alpha-rhythm. This reaction might become extinct in the course of the application of the stimulus and it might be re-established when a new stimulus is applied (Novikova, Sokolov, 1956).

The fact of the coincidence of regularities governing the extinction and the disinhibition of the blockade and alpha-rhythm activation with such direct indicators of the orienting reflex, as the eye movement, the turn of the head, etc., gives us the grounds for classing the above-said electroencephalogram reactions with the system of the orienting reflex described by I.P. Pavlov (1947) as the "What is it?" reaction.

An analysis of the relation between the alpha-rhythm blockade with the other components of the orienting reaction, proves that besides the features in common every component enjoys a degree of independence which is manifested in individual differences in the response to one and the same stimulus.

A study of various components of the orienting reaction in

100 persons that was carried out in our laboratory by U-Bao-Hua, has revealed that the first presentation of the sound stimulus (1,000 cps 50 db) induces the alpha-rhythm blockade of the occipital area in 85 men, the Rolandic Rhythm blockade in 53, skin-galvanic response in 95, the eye movements in 42, an alteration of breathing in 63, and an increase in the digital flexors' tonus in 1 person only. The simultaneous appearance of all the recorded components (excepting muscular reaction), was observed in 11 tested persons. Individual components were revealed in various combinations in all of the tested individuals.

Hence, while the initial presentation of the sound, in the case of one tested individual induced the entire complex of reactions, and only one, two or three components in another tested individual. The extinction rate of the various components in different test persons also varied. The absence of one component while the other components are retained, indicates the possibility of specialisation in the excitation of the orienting reflex.

2. The Efferent Concentration of Excitation During the Extinction of the Orienting Response.

A comparison between the effect induced by the light and tactile stimulus proves that the extinction rate of various components of the orienting reaction is subject to the quality of the stimulus. The initial presentations of light induces the entire complex of the orienting reaction including the alpha-

rhythm blockade of the occipital and motor areas of the cortex. As the presentation of light continues a greater stability is shown by the components associated with optic analyser. Thus, during the presentation of light the changes in the respiration, skin-galvanic reaction and the alpha-rhythm blockade of the motor area becoming extinct after two or three presentations, the movement of the eyes (when the side light source is used) may continue for five or ten presentations while the alpha-rhythm blockade of the occipital area may continue even after scores of presentations. In a number of cases a stable alpha-rhythm blockade may be observed even at hundreds of presentations of light stimuli which are close to the threshold. (Mikhalevskaya, 1957).

The relations in case of the tactile stimulus are different: here the occipital alpha-rhythm blockade disappears after 2-5 presentations while the skin-galvanic reaction and the Rolandic rhythm blockade are retained for 10-15 presentations. The Rolandic rhythm blockade and the skin-galvanic reaction proved to be even more stable during the presentation of the proprioceptive stimulation (Rogot, Voronin, Sokolov, 1958). It follows that the disappearance of the peripheral responses which are remote from the stimulated analyser and the more stable behaviour of the responses induced by an adequate stimulus coincides with the concentration of the alpha-rhythm blockade.

Inasmuch as the extinction of a number of peripheral

responses preceeds the disappearance of the changes in the cortical part of the stimulated analyser, their inhibition should not be explained by the blockade of impulses in the periphery of the analyser as is ventured by Galambos (1956), Jouvet and Hernandez-Peon (1957). This inhibition is equally inconceivable in the efferent mechanisms of the eye-movement or the skin-galvanic reactions since the change of the stimulus is accompanied by the reinstatement of these responses which is impossible when the working organ itself is in a state of inhibition.

It may be assumed that the inhibition of various components is localised on ^{the} pathways linking the given afferent system with the nuclei of the reticular system which participates in the orienting reflex activation mechanism.

3. The Afferent Generalisation in the Orienting Response Extinction.

The change of the stimulus (a variation in the position of the light source, in the sound frequency, in the point of the administration of the tactile stimulation of the skin) entails the reinstatement of the recorded response (Sokolov, 1955, 1958). This requires a certain measure of the variation of the new stimulus from the one presented earlier. The greater the difference, the greater the response within a certain range, the greater the number of components it includes. If only one, always the

same, stimulus is presented in an extinction test, then the reinstatement of the response may be observed also when the stimulus differs from the standard by a value approximating the difference threshold. Ordinarily, however, the extinction proceeds in a generalised manner and covers the zone of related stimuli. The degree of extinction generalisation mounts with the repetition of tests incorporating various stimuli. We have observed generalised extinction in the optic, auditory and skin-analysers. It manifested itself by a phenomenon when the orienting response after becoming extinct to one of the stimuli was no longer induced by a number of related stimuli.

A specific investigation carried out by the method of local stimulation of the retina by a projection perimeter, revealed that following the extinction of the alpha-rhythm blockade response to light 40° (falling to the right from the fixation point), the 45° light did not induce the response, the 50° induced a weak response while the 60° and the 70° induced well expressed responses.

The generalisation zone on both sides of the basic point was 10° . In the experiments which followed, the extinction zone was extended to 20° .

The change in the stimuli, the variation of the experiment conditions - all entails a dislocation of the achieved degree of generalisation and the stimuli which ceased to induce any response, regain their effectiveness.

It has been shown by the experiments that inhibition is appreciably dependent on the properties of the afferent system. This is exhibited by the fact that the inhibition during the stimulation of the auditory system, the skin and the retina may spread to the adjacent points in keeping with to the somatopleic projection principle.

Assuming that there are pathways from the different points of the receptor surface leading to the different departments of the reticular system we may combine the data covering the efferent concentration of the excitation and that of the afferent irradiation of the inhibition process. Then the selective inhibition may be conceived as a drop in the excitability along the pathways linking various points of the receptor surface with the reticular system. In this case, the excitation induced by stimulating one point of the receptor surface will reach the reticular system while the stimulation of another point related to the stimulus which was employed in the extinction shall not be effective.

4. The Impossibility of Reducing the Extinction of the Orienting Response to the Excitability Drop in Certain Points of the Afferent System.

and
Repetitive numerous presentations of the stimulus increase the threshold of the orienting response evocation. This is exemplified by the fact that with the increase of extinction ever stronger stimuli have to be used to induce the

blockade reaction (Sokolov, Danilova, Mikhalevskaya, 1955; Sokolov, 1958). A question presents itself whether the extinction of the orienting response is exhausted by the local stimulation drop of the pathways leading to the reticular system as can be supposed in the case of inhibition of the alpha-rhythm blockade from a definite point of the retina.

Special experiments have to be referred to to provide an answer to this question. Let us resort to a sufficiently strong repetitive sound stimulus (1,000 cps 70 db), and represented so that it would gradually cease to induce the alpha-rhythm blockade. If the disappearance of the response is due only to the excitability drop, it is clear that even a weaker stimulus should not induce a response since it will be below the excitability threshold. However, the alpha-rhythm blockade as a component of the orienting response occurs even with the weakening of the stimulus. This concerns also the action of the light stimuli.

To enable the appearance of a response during the weakening of the stimulus with regard to a definite level of the initial agent intensity it is imperative that : a) there remain a trace of the repetitive stimulus; b) there take place a comparison of the new stimulus with the trace left in the nervous system by the preceding presentations of the stimulus. For the sort of selective extinction of the orienting reflex we should suppose the possibility of the retention of a sufficiently high excita-

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bility in the afferent system necessary for an adequate appreciation of the true intensity of the newly used stimulus. If the response to a weaker stimulus is due to its deviation from a given standard, a supposition may be offered that besides the direct stimulation through the collaterals leading to the reticular system it might be stimulated by the impulsion which occurs as a result of the non-coincidence of the dynamic stereotype which occurred earlier in the nervous system and the flow of impulses which arrives due to the action of the new stimulus.

The concept of the construction of a "nervous model", in the brain formations, of a stimulus which has been repeatedly represented during the extinction of the response is corroborated by a series of other experimental findings. Thus, if the sound stimulus of a definite intensity, duration and quality, be applied to a tested person with a strictly permanent frequency of the representations then after a definite number of the applications the alpha-rhythm blockade as has been said above, disappears. However, it occurs not only during the weakening or the intensification of the stimulus, but also during a sudden omission in the representation of the stimulus in the usual time. The occurrence of the alpha-rhythm blockade may be observed at a sudden shortening (replacing the stimulus which usually followed), or at a lengthening of the stimulus representation (there where the stimulus was non-existent formerly). It

follows that the "nervous model" besides the intensity parameter, has a time aspect as well.

An analysis of the described experiments gives grounds for a supposition that the stimulation of the orienting reaction is determined by the impulsion occurring in the centres due to the comparison of the stimulus with the "nervous model" which takes shape during the stimulation. Under definite terms, the orienting reflex as the activation response is not included provided the comparison returns of the stimulus and the "nervous model" indicate their coincidence. Apparently, with the repeated presentation of the stimulus under similar conditions when this coincidence between the stimulus and the "nervous model" is achieved, the impulses which usually arrive to the reticular system directly, are inhibited by reflex action and do not determine the ultimate result of the response.

3. The Cortical Mechanisms of the Orienting Response Extinction.

The concept of a "nervous model" which develops due to a multiple representation of the stimulus does not describe the localisation of the modelling and comparison processes. A series of experimental data, however, give grounds to suppose that the cortex as the organ of the most subtle integration of specific forms of excitation plays the main part in the selective extinction of the orienting responses in man.

This is brought out by the experiments which were made to study the orienting responses to a consecutive integrated stimulus incorporating the sound, light and tactil stimulus. With an increase in the presentations of the above-said complex, the orienting responses to its component parts were gradually becoming extinct. If later on, only the sound stimulus was presented, however, then orienting responses including the alpha-rhythm blockade occurred in place of the light and tactil stimulation. The same phenomenon has been observed if the light (or the tactil stimulus) were employed outside of the usual combination with the other stimuli. In this case the alpha-rhythm blockade occurred as a result of the dislocation of the stereotype which combined the functions of several analysers. In this case, the diverse analysers are represented as having equal rights and only their combined, integrated activity may provide the grounds for the construction of the "nervous model" which later on would determine the action of the employed stimuli.

There are, however, even more convincing data describing the part played by the cortex in the extinction mechanism of the orienting reflex and of its electroencephalographic component in particular. This is exemplified by our laboratory experiments of orienting responses extinction to verbal stimuli (Murushevsky, 1957; Vinogradova, 1957). Additional experiments have shown that when the alpha-rhythm blockade became extinct

to one group of semantically close but phonetically different words, the representation of a word with a new meaning had again induced the orienting response. Against the background of the generalised extinction of the responses to indifferent words the responses associated with the experiment and also the responses to the proper name and to the words of a particular significance for the tested person remained stable.

It is known that verbal stimulus may most materially alter the entire pattern of the electroencephalogram. Thus the command "don't be drowsy" against the background of the extinct responses to other words, induces a long tonic form of the changes in the EEG. The effect of word stimuli with regards to the alpha-rhythm blockade response is first of all subject to the meaning of the word. In this case, speaking of the "nervous model" associating with the words by some definite indication we cannot fail acknowledging the leading part of the specific cortex formations in bringing about the extinction and the stimulation of the alpha-rhythm blockade.

We shall now discuss the way the orienting reflex is made extinct from the point of view of the participation of the comparison mechanisms of the "nervous model" and the new stimulus. With the representation in time of a definite stimulus, there originates a "nervous model" of the stimulus and simultaneously there develops a

conditioned reflex designed to blocking the impulses arriving to the reticular system via the collaterals.

This concept is based on I.P.Pavlov's findings about the relation between the extinction of the orienting reflex and the mechanisms of the conditioned inhibition.(Pavlov,1947).

In this conditioned reflex the conditioned stimulus is provided by some definite property of the stimulus intensity duration, or some other quality while the unconditioned reinforcement is provided by the unconditioned inhibition which apparently occurs in the reticular system when there is a sufficiently long action of any stimulus and is expressed by the fact that having occurred at the instant of the presentation the response disappears against the background of its continuous operation. The elaboration of a conditioned reflex facilitates the development and the occurrence of this inhibition. Thus, with a continuous presentation of a sound or light stimulus, we may observe the gradual shortening of the depression time and the moment of the alpha-rhythm reinstatement approaches the beginning of the stimulus action. When the stimulus is changed the response becomes longer again, because the mechanism of the preliminary conditioned-reflex limitation or suppression of the stimulation in this case does not operate. In case of a sudden shortening (or omission), of the stimulus the excitation of the reticular system is effected by the central mechanism where the major part is played by the non-coincidence in time of the

"nervous model" and the system of the presented stimulations.

6. Sleep Inhibition Development During the Extinction of the Orienting Reflex.

During the continuous employment of a stimulus not only does the impulse blocking develop and the spread of impulses in the reticular system is restricted, but there also takes place an alteration in the functional state of the cortex.

We might distinguish several stages in the alpha-rhythm blockade extinction. At first there is a gradual decrease in the responses. Then, the absence of the blockade responses becomes quite stable. As the stimulus is further applied there begins to develop a state of drowsiness, the alpha-rhythm disappears in the background and then in response to the very sound there appear the alpha-rhythm activation. At the same time there takes place the reinstatement of the skin-galvanic, eye movement and respiratory components. A characteristic feature of the reinstated responses is their greater stability and that they are not as easily put out as the responses induced in the early stages of the experiment. However, these reactions become extinct as the presentation of the stimuli continues. During this process we can usually observe an increase in the theta and delta oscillations and of the spindles, indicating that the sleep inhibition is becoming deeper.

The analysis of the above mentioned experiments reveals that inhibition as a functional state of the bulk of cortical cells does not coincide with inhibition as a regulation of the ~~excitatory~~ process during the delaying of certain responses. It is particularly important that there exists a stage when the deepening of inhibition as a state of the cortical cells is accompanied by the disinhibition of the extinct responses. This inconsistency testifies in favour of a supposition that the extinction of an orienting reflex in an alert and active state takes place with the participation of the cortical conditioned-reflex bonds which block and restrain the action of the stimulus. Moreover, the functioning of these conditioned bonds by itself necessitates a definite degree of the activity of the cortical cells.

The changes in the functional state of the cortical cells during the extinction of the orienting reflex may be traced by the peculiar changes in the spectrum of the electroencephalogram, on the one hand, and the change in "driving response" to a rhythmical light stimulus on the other. Thus against the background of well expressed beta oscillations, the action of the rhythmic stimulus of 9 cps evokes the appearance of 18 and 27 cps in the cortex. Moreover in a number of cases the oscillations of the main frequency of 9 cps in the cortex may be absent.

With the continuation of the stimulation and with the development of deeper inhibition slow waves appear in the

EEG spectrum while the "driving", coinciding at times with the appearance of subharmonics, includes elements of the alpha-rhythm activation. The waning alters the background EEG and simultaneously alters the "driving" effect which is again described by the appearance of high harmonics (Danilova, 1957; Sokolov, 1958). Thus, we should distinguish two forms of inhibition in the extinction of the alpha-rhythm blockade: a) the conditioned-reflex regulation of carrying the excitation to the reticular system and b) the drop in the level of the functional state of the bulk of cortical cells.

7. The Orienting Reflex Extinction Mechanisms.

We can distinguish two basic ways of stimulating the blockade response as a component of the orienting reflex: the first way is to conduct the stimulation via the collaterals leading from the afferent pathway to various nuclei and levels of the reticular formation. The other way is associated with the passage from the cortex to the reticular formation of signals which either inhibit or intensify its activity. This way ensures the responses associated with the action of complex stimuli which require the cortical integration of the stimulation.

Russinov and Smirnov (1957) presenting the data of the experiments with signal and verbal stimuli made a specific

indication of the relation between the electrical responses of the brain and the cortex functions.

As has been shown by Sharpless and Jasper (1956), we can distinguish a selective extinction of reactions to involved complexes among the diverse forms of the arousal response extinction. When the cortex is removed these disappear and are not reinstated at a later date. These findings corroborate the data obtained by Roland (1957), who proved the impossibility of a selective extinction of the arousal responses to various complexes of sounds after the removal of the cortex.

Our findings indicate that the extinction of the orienting reflex takes place with the participation of the developed conditioned reflex inhibition where the information conveyed by means of a specific formation and integrated at the cortex level seemed to play the main part.

This conditioned-reflex cortical regulation of the activation system itself shows that it is impossible to regard the reticular formation as the main substratum of the conditioned-reflex bonds in man. The duration, strength and nature of the excitation of the reticular formation as the main source of the activating influences also occurs by itself with the participation of the cortex.

Conclusions.

I. The electroencephalographic response to various stimuli is a component of a complex orienting response including vegetative and somatic components.

2. The varying extinction rate of different orienting response components indicates the existence of inhibition which cannot be reduced to the blocking of pulses on the afferent pathways and restricting the spread of the excitation in the non-specific formation limiting it to the local activation of the stimulated analyzer.

3. The possibility of a selective extinction of the electroencephalographic response to a restricted group of stimuli is an indication of connections between every point of the receiving area and the reticular formation.

4. The peculiarities of the extinction of the electrical response of the brain to complex and verbal stimuli shows that the cortex inhibitory conditioned-reflex mechanisms which restrict the stimulation of the reticular formation, participate in the extinction process.

5. The peculiarities of the appearance of electroencephalographic responses during the change of the stereotype of the presenting stimulations indicates that besides the passage of the excitation along the collaterals, there exist the cortico-reticular pathways of the excitation transit which originates during the non-coincidence of the "nervous model" and the new stimulus.

6. The role played by the cortex in the extinction of the electroencephalographic response is corroborated by the

existing disinhibition of the orienting responses at the first stage of the sleep inhibition, following the extinction of the alpha rhythm blockade to the same stimulus.

7. In the extinction of the orienting reflex a distinction should be made between the inhibition as a reflex regulation which restricts the action of the stimulus to the non-specific formation and the inhibition as a definite level of the functional state of the bulk of the cortical cells.